THE LARVAL DEVELOPMENT OF *CARCINUS MAENAS* (L.) AND *C. MEDITERRANEUS* CZERNIAVSKY (CRUSTACEA, BRACHYURA, PORTUNIDAE) REARED IN THE LABORATORY

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THE LARVAL DEVELOPMENT OF *CARCINUS MAENAS* (L.) AND *C. MEDITERRANEUS* CZERNIAVSKY (CRUSTACEA, BRACHYURA, PORTUNIDAE) REARED IN THE LABORATORY

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SYNOPSIS

The larval stages of the shore crab *Carcinus* reared from females collected in British waters are compared with those reared from a female collected in Tunisia and slight, but consistent, differences are noted between them. The Atlantic and Mediterranean populations of *Carcinus* have recently been separated as distinct species on the basis of adult characters, the name *C. maenas* (L.) being applied to the Atlantic form and *C. mediterraneus* Czerniavsky to the Mediterranean form. Although the larval differences support the possibility that the two populations are genetically distinct, if, as presently seems to be the case, they are found to be totally allopatric with no chance of interbreeding in areas of overlap, it is suggested that they should be accorded only subspecific status, a course which would reflect both their close relationship and geographical separation.

INTRODUCTION

In the first half of this century the larval stages of the crabs of north-western Europe were better known than those of any other region, mainly as a result of Lebour's (1928) classic work on the Plymouth Brachyura. Lebour's descriptions, however, were often inadequate and more recent studies on crabs from other areas, and particularly those based on reared material, have provided more detailed accounts of the larval development than those available for British species.

In 1969 therefore, a research programme was started at the British Museum (Natural History) with the intention of rearing as many British crabs as possible and providing detailed descriptions of all their developmental stages. As a result of this programme descriptions of the sponge crab *Dromia personata* (L.), and of the masked crab *Corystes cassivelaunus* (Pennant), have already been published (Rice, Ingle & Allen, 1970 ; Ingle & Rice, 1971) and although crabs of any of the fourteen families represented in British waters will be reared and described as and when ovigerous females become available, efforts are now being concentrated on the swimming crab family Portunidae and the spider crab family Majidae and the programme has been expanded to include the rearing of Mediterranean species belonging to these families.

Apart from the spider crabs (Majidae) the portunids are better represented around British coasts than any other family of crabs, fourteen species and five genera having been recorded. This paper deals with the commonest of these species, *Carcinus maenas* (L.) and with the closely related Mediterranean form, *C. mediterraneus* Czerniavsky.

The common shore crab or green crab, *C. maenas*, is found in the Atlantic on all types of shore and sublittoraly to depths of 200 m, from northern Norway to

Mauritiana in the east and from Nova Scotia to Brazil in the west (Christiansen, 1969). It is therefore not surprising that it was one of the first crabs to have its development investigated, the first zoea having been hatched and described by Couch in 1840.

Since that time there have been many accounts of the various larval stages of *Carcinus*, those by Williamson (1900, 1903) being by far the most detailed and complete (see Lebour, 1928, for earlier references). Williamson hatched the first zoea which moulted to the second stage, but he obtained the later zoeae and the megalopa from the plankton and it was not until 1967 that the species was reared in the laboratory with any degree of success (Williams, 1967). Williams, however, reared *Carcinus* mainly for behavioural studies and did not describe the larval stages which she obtained, so that there is still no published account of the species' development based on reared material.

In 1971 we succeeded in obtaining all four zoeae, the megalopa and the young crab stages of *Carcinus maenas* from laboratory-reared material. At that time *Carcinus* was being used simply as a test animal to assess the efficiency of the rearing method, the shore crab having been chosen for this purpose because of the relative ease with which ovigerous females could be obtained. Compared with many other British crabs the larvae of *C. maenas* were well known and a new account did not seem to be warranted, even though the description could now be based on a complete series of reared stages. However, Williamson's papers were published in a journal which is not now readily accessible to many workers and when one of us (R. W. I.) reared the larval stages of *C. mediterraneus* from a female collected in Tunisian waters, it seemed worth while to publish a comparative account of the development of these two closely related species.

MATERIAL AND METHODS

Larvae were reared from two female *Carcinus maenas*, one collected at Plymouth, Devon, in April 1971 (B.M. reg. no. 1974:331) and the other at Brighton, Sussex, in May 1973 (B.M. reg. no. 1974:332), and from one female *C. mediterraneus* collected at the northern Punic Port, Salammbo, Tunis in February 1974 (B.M. reg. no. 1974:330).

The ovigerous crabs were maintained in sea water treated with 0·01 N EDTA and in each case hatching occurred over a 48 h period. All larvae were reared at 15 °C (but see below) in sea water treated with EDTA (0·01 N), benzylpenicillin (50 000 units/litre) and reduced glutathione (0·001 M), the last additive acting as a feeding stimulant. Every other day the culture water was changed and at the same time the larvae were fed on freshly hatched *Artemia* nauplii.

The Plymouth *C. maenas* larvae were reared in compartmented plastic trays, while the Brighton *C. maenas* and the *C. mediterraneus* were reared in 'mass culture' polythene jars using a technique similar to that described by Cook (1969) for rearing penaeid larvae. In these cases 300–400 larvae were placed into each container (see Fig. 1) and the large *Artemia* moults and dead larvae were removed when the water

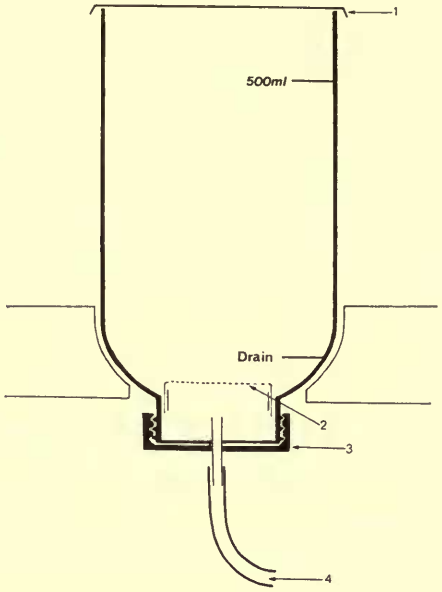

FIG. 1. Mass-culture vessel made from a 500 ml polythene bottle and used to rear *Carcinus*. 1, lid ; 2, nylon mesh secured by a collar ; 3, screw-on jar cap ; 4, air supply and drain tube.

level was reduced to the 'drain' line at each water change. A gentle air stream induced sufficient water movement in the jars to keep the larvae circulating.

Survivals of both the tray-reared and mass-cultured *C. maenas* larvae were very high, up to 68 per cent of the stage 1 zoeae reaching the first crab stage. During the *C. mediterraneus* culture period, however, an air-conditioner breakdown resulted in several days of oscillating water temperatures reaching 25 °C. Survivals were therefore poor, only two animals reaching the first young crab stage and neither surviving to the next moult.

The larvae and moults were preserved in 70 per cent ethanol, and cleared and dissected in lactic acid. Drawings and measurements were made with the aid of a *camera lucida*. The measurements taken were (a) the distance between the tips of the dorsal and rostral spines (*T.T.*), (b) the rostral spine length (*R.S.*) from the tip of the spine to the lower margin of the eye, (c) the dorsal spine length (*D.S.*) and (d) the carapace length (*C.L.*) from between the eyes to the posterio-lateral carapace margin.

RESULTS

Adults

Until relatively recently the genus *Carcinus* was considered to contain only the single species, *C. maenas*, which was recorded from the Atlantic, the Mediterranean and, probably as an introduced form, from the Indo-West Pacific region.

Demeusy & Veillet (1953) pointed out differences between the Atlantic and Mediterranean populations and Holthuis & Gottlieb (1958) resurrected the name *C. mediterraneus* Czerniavsky for the Mediterranean form.

Four of the features mentioned by Zariquièy Alvarez (1968) as distinguishing *C. mediterraneus* adults from those of *C. maenas*, that is the less sharp anterio-lateral carapace teeth, the denser setation of the anterio-lateral carapace margins, the sharper carpal tooth on the cheliped and the more pronounced anterio-external angle of the merus of the third maxilliped, are not apparent in the females from which the larvae reported in this paper were obtained. There are, nevertheless, good morphological distinctions between the females and these are listed in Table 1 and illustrated in Plate 1.

TABLE 1

Differences between the female *C. maenas* and *C. mediterraneus* from which the larvae were reared (see also Plate 1)

C. maenas	*C. mediterraneus*
1. Carapace relatively broad (Brighton spec. *C.L.* 29·5 mm, *C.W.* 39·0 mm, *C.W./C.L.* 1·32 ; Plymouth spec. *C.L.* 40·0 mm, *C.W.* 51·5 mm, *C.W./C.L.* 1·29) (Plate 1A)	Carapace relatively narrow (*C.L.* 27·55 mm, *C.W.* 34·5 mm, *C.W./C.L.* 1·25) (Plate 1D)
2. Carapace dorsal surface relatively rough to touch	Carapace dorsal surface smooth
3. 5th (posterior) pair of anterio-lateral teeth directed forwards	5th pair of anterio-lateral teeth directed more or less outwards
4. Front does not protrude and is not setose (Plate 1A)	Front protrudes and is setose (Plate 1D)
5. Carapace regions not strongly elevated and, when viewed from behind, carapace relatively flat (Plate 1B)	Carapace regions elevated, and carapace vaulted (Plate 1E)
6. Outer margin of cheliped carpus not setose (Plate 1C)	Outer margin of cheliped carpus setose (Plate 1F)

Larval stages

The larvae of the two forms are very similar, particularly in the zoeal stages where the only morphological distinctions noted were the relative lengths of the dorsal and rostral carapace spines. With the exception of the dimensions, therefore, the following descriptions of the zoeae apply both to *C. maenas* and *C. mediterraneus*.

First zoea

Dimensions

Carcinus maenas: *T.T.* 1·36–1·44 mm, mean (10 specimens) 1·38 mm ; *C.L.* 0·47–0·53 mm, mean 0·50 mm ; *D.S.* 0·53–0·57 mm, mean 0·55 mm ; *R.S.* 0·46–0·51 mm, mean 0·49 mm ; ratio *D.S./R.S.* 1·04–1·22, mean 1·12.

Carcinus mediterraneus: *T.T.* 1·36–1·43 mm, mean (10 specimens) 1·38 mm ; *C.L.* 0·53–0·57 mm, mean 0·56 mm ; *D.S.* 0·58·0·63 mm, mean 0·60 mm ; *R.S.* 0·40–0·43 mm, mean 0·41 mm ; ratio *D.S./R.S.* 1·34–1·57, mean 1·47.

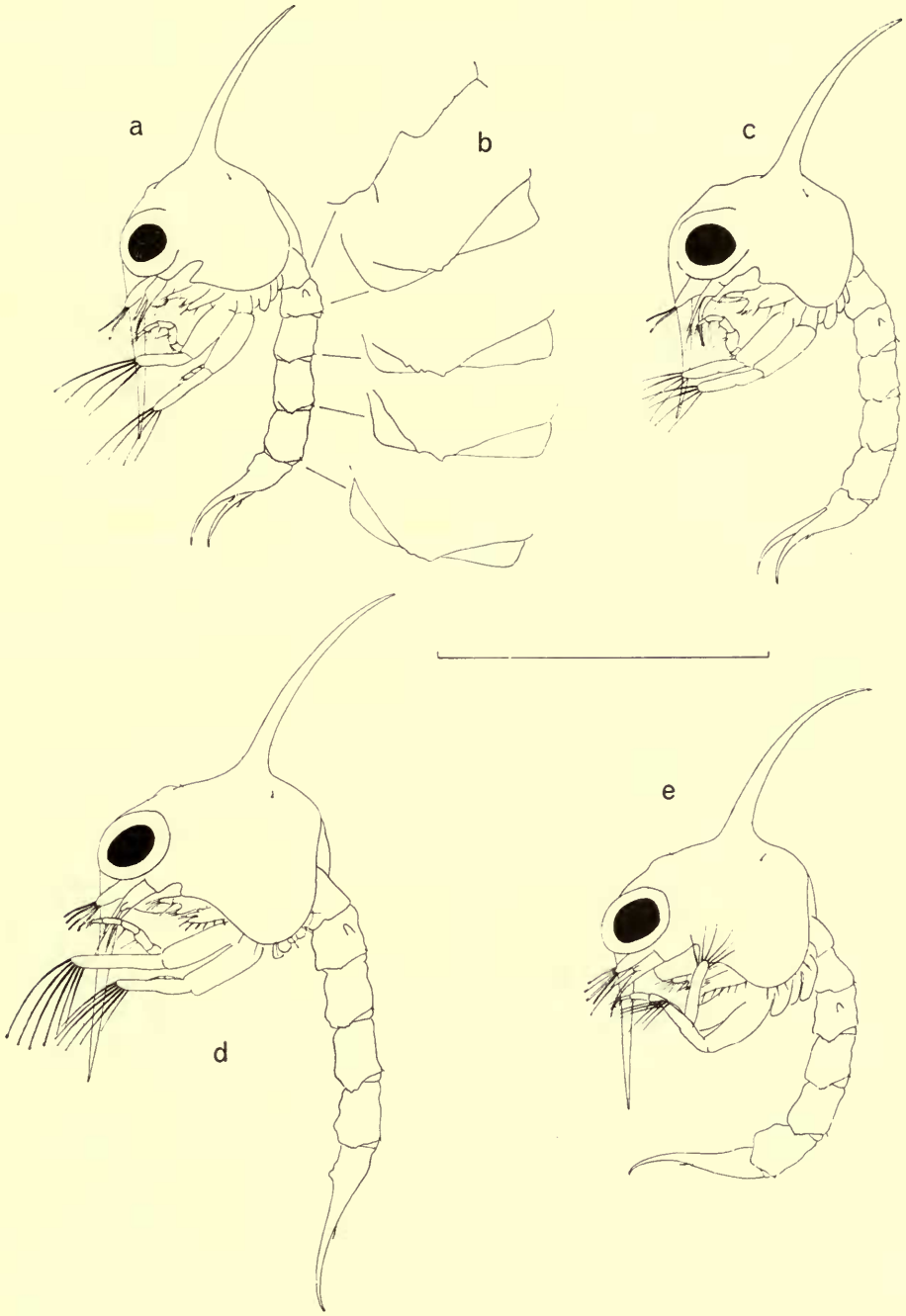

FIG. 2. *Carcinus* zoeal stages I and II : (*a*) *C. maenas* stage I ; (*b*) detail of posterio-lateral angles of abdominal somites ; (*c*) *C. mediterraneus* stage I ; (*d*) *C. maenas* stage II ; (*e*) *C. mediterraneus* stage II. Bar scale represents 1·0 mm.

Carapace (Fig. 2*a*, *c*) : Well-developed backwardly curved dorsal spine and straight or slightly curved rostral spine, but no laterals. A low anterior papilla between the eyes and a pair of small setae lateral to and slightly behind the dorsal spine.
Eyes : Partly fused to carapace.
Antennule (Fig. 3*b*) : Unsegmented, with two terminal aesthetascs and two setae.
Antenna (Fig. 3*c*) : Spinous process about half as long as rostral spine in *C. mediterraneus* and somewhat less in *C. maenas*, with two rows of spinules on the distal two-thirds. Exopod about half as long as spinous process, with one long and one short terminal spine each with minute spinules at their bases. Endopod represented by a small bud.
Mandible : Without palp.
Maxillule (Fig. 3*d*) : Endopod two-segmented, with 6 and 1 setae respectively. Basal endite with 4 setose spines and 1 seta, coxal endite with a total of 5 spines and setae.
Maxilla (Fig. 3*e*) : Endopod, basal endite and coxal endite each bilobed, with 5+3, 4+4 and 3+3 setae respectively. Scaphognathite with 4 marginal setae and a long plumose posterior projection.
First maxilliped (Fig. 3*f*) : Basis with 8 or 9 medial setae. Five-segmented endopod with 2, 2, 1, 2 and 4+1 setae respectively. Exopod with 4 natatory setae.
Second maxilliped (Fig. 3*g*) : Basis with 4 medial setae. Three-segmented endopod normally with 1, 1 and 5 setae, though the small lateral seta on the terminal segment may be absent. Exopod with 4 natatory setae.
Third maxilliped and pereiopods : Unarmed, unsegmented buds.
Abdomen (Fig. 3*a*) : Five somites and telson. Somite 2 with forwardly directed dorso-lateral knobs. Somites 2–5 each with rounded posterio-lateral margins with small teeth, and with a pair of small setae near the posterior margin. Telson with 3 pairs of setose processes on the posterior margin, and each fork with one large and one small dorsal spine and a very slender lateral spine.

Second zoea

Dimensions

Carcinus maenas : *T.T.* 1·58–1·85 mm, mean (8 specimens) 1·75 mm ; *C.L.* 0·60–0·70 mm, mean 0·67 mm ; *D.S.* 0·55–0·70 mm, mean 0·67 mm ; *R.S.* 0·52–0·65 mm, mean 0·58 mm ; ratio *D.S./R.S.* 1·06–1·26, mean 1·15.

Carcinus mediterraneus : *T.T.* 1·44–1·56 mm, mean (7 specimens) 1·46 mm ; *C.L.* 0·60–0·70 mm, mean 0·62 mm ; *D.S.* 0·58–0·63 mm, mean 0·59 mm ; *R.S.* 0·36–0·48 mm, mean 0·43 mm ; ratio *D.S./R.S.* 1·30–1·69, mean 1·38.

Carapace (Fig. 2*d*, *e*) : A pair of small setae added between the dorsal spine and the anterior papilla. Posterio-lateral margins with 4–6 setae. Otherwise as in the first stage.
Eyes : Now stalked.
Antennule (Fig. 3*h*) : Unsegmented, with 4–6 terminal aesthetascs and 1 or 2 setae.
Antenna (Fig. 3*j*) : Endopod bud slightly larger than in first stage, otherwise unchanged.

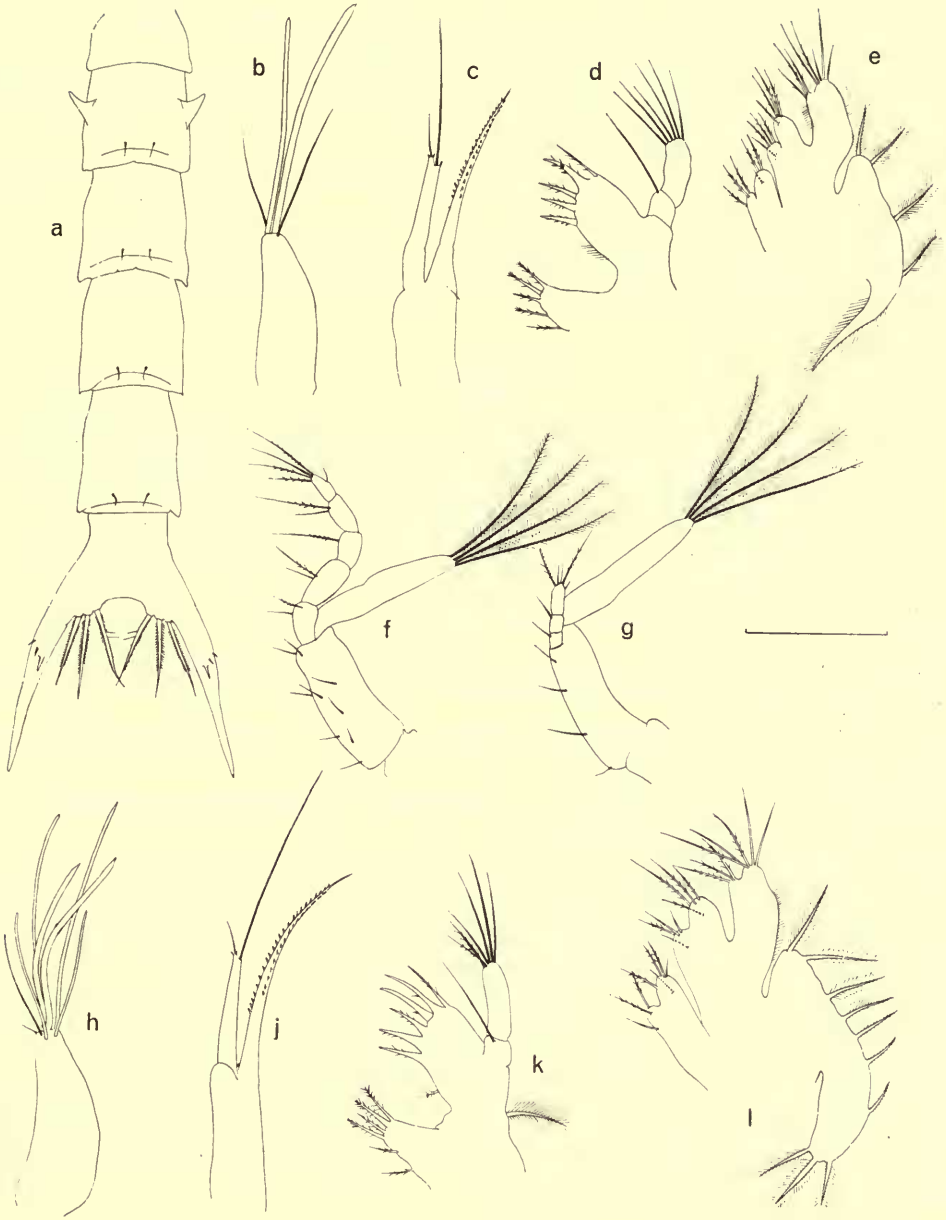

FIG. 3. *Carcinus* zoeal stages I and II : (*a*) abdomen, stage I ; (*b*) antennule, stage I ; (*c*) antenna, stage I ; (*d*) maxillule, stage I ; (*e*) maxilla, stage I ; (*f*) first maxilliped, stage I ; (*g*) second maxilliped, stage I ; (*h*) antennule, stage II ; (*j*) antenna, stage II ; (*k*) maxillule, stage II ; (*l*) maxilla, stage II. Appendages *b*, *c*, *e*, *k* and *l* are drawn from *C. maenas* specimens and the remainder from *C. mediterraneus*. Bar scale represents 0·2 mm for *a*, *f* and *g*, and 0·1 mm for the rest.

Mandibles : Unchanged.
Maxillule (Fig. 3*k*) : Basal endite with 6 or 7 spines and setae, coxal endite with 5 or 6. Exopod seta now present, endopod unchanged.
Maxilla (Fig. 3*l*) : Scaphognathite now with 9–11 marginal setae, the posterior projection no longer being apparent. Endopod and basal endites unchanged, but coxal endite may now carry an extra seta.
First and second maxilliped (Fig. 2*d*, *e*) : Exopods with 6 natatory setae ; otherwise unchanged.
Third maxilliped and pereiopods : Still unsegmented and unarmed buds.
Abdomen : Unchanged except that the two smaller spines on each telson fork are either reduced or absent.

THIRD ZOEA

Dimensions

Carcinus maenas : *T.T.* 2·13–2·15 mm, mean (3 specimens) 2·14 mm ; *C.L.* 0·79–0·85 mm, mean 0·82 mm ; *D.S.* 0·80–0·85 mm, mean 0·82 mm ; *R.S.* 0·70–0·80 mm, mean 0·73 mm ; ratio *D.S./R.S.* 1·06–1·21, mean 1·14.
Carcinus mediterraneus : *T.T.* 1·93 mm ; *C.L.* 0·82 mm ; *D.S.* 0·77 mm ; *R.S.* 0·51 mm ; ratio *D.S./R.S.* 1·52.

Carapace (Fig. 4*a*, *b*) : Posterio-lateral margins with 8–12 setae, otherwise unchanged.
Antennule (Fig. 4*d*) : Three or four terminal and one sub-terminal aesthetascs, plus 1 or 2 terminal setae.
Antenna (Fig. 4*e*) : Exopod about two-thirds length of spinous process ; endopod slightly shorter.
Maxillule (Fig. 4*f*) : Basal and coxal endites with 9 and 6 spines respectively ; 1 or 2 exopod setae ; endopod unchanged.
Maxilla (Fig. 4*g*) : Endopod, basal endite and coxal endite with 4–5+3, 3–5+4 and 3–4+3 setae respectively. Scaphognathite with 19 or 20 marginal setae.
First maxilliped (Fig. 4*a*, *b*) : Basis and endopod unchanged except that terminal segment may carry 4 or 5+1 seta ; exopod with 8 natatory setae.
Second maxilliped (Fig. 4*a*, *b*) : Exopod with 8 natatory setae ; otherwise unchanged.
Third maxilliped : Now bilobed, but still unsegmented and unarmed.
Pereiopods : Unarmed, unsegmented buds, first pair cheliform.
Abdomen (Fig. 4*a*, *b*) : Somite 1 with single median dorsal seta, somites 2–5 with well-developed pleopod buds, somite 6 separated from the telson and carrying small uropod buds. Telson forks each usually with one large and one small dorsal spine, though the latter may be absent.

FOURTH ZOEA

Dimensions

Carcinus maenas : *T.T.* 2·20–2·50 mm, mean (5 specimens) 2·37 mm ; *C.L.* 1·02–1·10, mean 1·06 mm ; *D.S.* 0·81–0·91, mean 0·86 mm ; *R.S.* 0·74–0·83 mm, mean 0·77 mm ; ratio *D.S./R.S.* 1·02–1·20, mean 1·11.

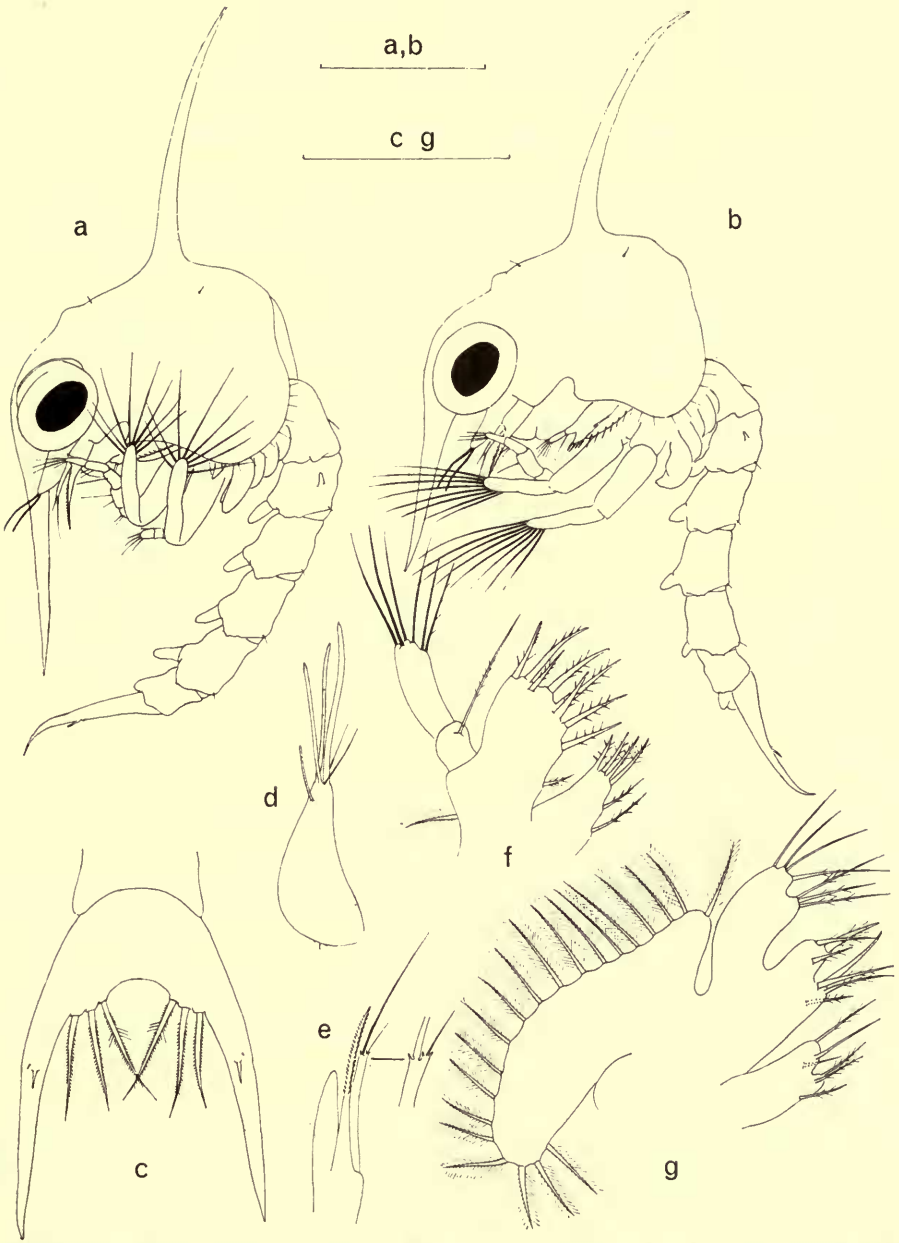

FIG. 4. *Carcinus* zoea stage III : (*a*) *C. maenas* ; (*b*) *C. mediterraneus* ; (*c*) telson, *mediterraneus* ; (*d*) antennule, *maenas* ; (*e*) antenna, *maenas* ; (*f*) maxillule, *mediterraneus* ; (*g*) maxilla, *mediterraneus*. Bar scales represent 0·5 mm for *a* and *b* and 0·25 mm for *c*–*g*.

Carcinus mediterraneus : *T.T.* 2·10–2·35 mm, mean 2·23 mm ; *C.L.* 0·90–0·99 mm, mean 0·95 mm ; *D.S.* 0·90–0·95 mm, mean 0·93 mm ; *R.S.* 0·67–0·72 mm, mean 0·70 mm ; ratio *D.S./R.S.* 1·32–1·34, mean 1·33.

Carapace (Fig. 5*a*, *b*) : Posterio-lateral margin now with 12–16 setae, otherwise unchanged.

Antennule (Fig. 5*d*) : Terminal seta and a total of 6–7 aesthetascs in three groups. Exopod bud present.

Antenna (Fig. 5*e*) : Endopod now equal or almost equal to spinous process.

Maxillule : Basal endite may have an additional spine, otherwise unchanged.

Maxilla (Fig. 5*f*) : Scaphognathite with 22–24 marginal setae. Setation of endopod and endites falls within the range in the third stage.

First and second maxillipeds : Exopods with 10 natatory setae, otherwise unchanged.

Third maxilliped and pereiopods : Large and with the beginnings of segmentation, but still unarmed.

Abdomen (Fig. 5*a*, *b* and *c*) : Pleopods now as long as succeeding abdominal somites. Telson forks with one large dorsal spine and usually with a minute second spine.

Megalopa

The megalopa stages of the two species are more easily distinguished than the zoeae. However, the differences noted involve only the pleopods, uropods and telson and with the exception of these features the following description, like those of the zoeal stages, applies both to *C. maenas* and *C. mediterraneus*.

Dimensions

Carcinus maenas : *C.L.* 1·26–1·40 mm ; *C.W.* 0·96–1·18 mm.

Carcinus mediterraneus : *C.L.* c 1·21 mm ; *C.W.* c 1·02 mm.

Antennule (Fig. 7*a*) : Dorsal flagellum of 4 segments, the distal 3 segments each with 3 or 4 aesthetascs. Terminal segment with 2 setae, penultimate segment with a lateral seta and with or without a medial seta. Ventral flagellum unsegmented with 4 terminal setae, and 1 or 2 subterminal ones.

Antenna (Fig. 7*b*) : Three-segmented peduncle carrying 3, 0 and 1 setae respectively. Flagellum of 7 segments, though the septum between segments 2 and 3 is indistinct. Flagellar segments 3, 5 and 7 each carry 4 setae.

Mandible (Fig. 7*e*) : Two-segmented palp with about 6 terminal setae.

Maxillule (Fig. 7*c*) : Endopod with 1 or 2 terminal setae ; basal endite with a row of 5–7 marginal spines and a total of about 11 setae, coxal endite with 7 or 8 setae.

Maxilla (Fig. 7*d*) : Scaphognathite with 37–44 marginal setae and with 5 or 6 setae on the surfaces of the blade. Endopod unarmed or with a single short seta. Lobes of the basal and coxal endites carrying 7, 6–7, 2 and 3–4 setae respectively.

First maxilliped (Fig. 7*f*) : Exopod two-segmented, with 2 setae on proximal segment and 3–5 on the distal segment. Unsegmented endopod with 4 or 5 marginal setae. Basal segment with 14–16 marginal and sub-marginal setae. Coxal endite with 5 or 6 setae. Well-developed triangular epipod.

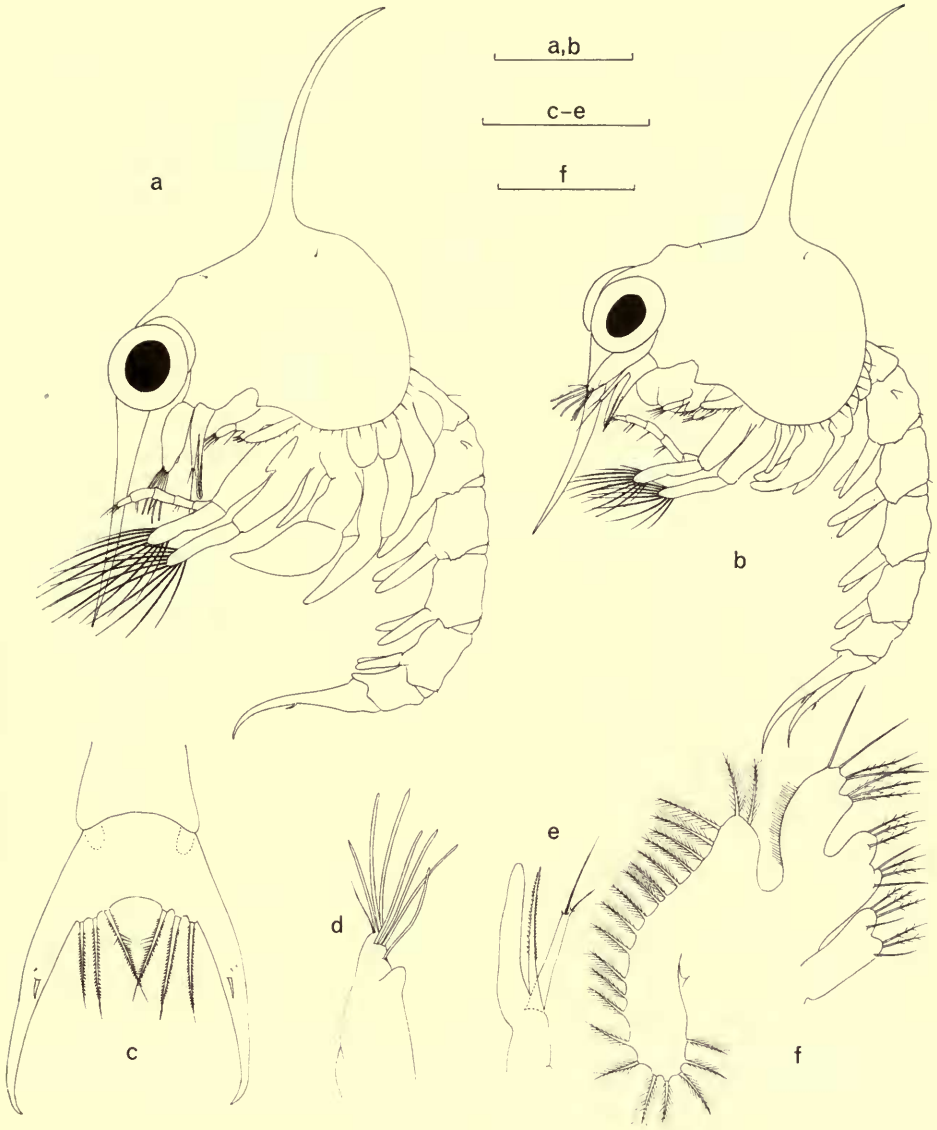

FIG. 5. *Carcinus* zoea stage IV : (*a*) *C. maenas* ; (*b*) *C. mediterraneus* ; (*c*) telson, *maenas* ; (*d*) antennule, *maenas* ; (*e*) antenna, *maenas* ; (*f*) maxilla, *mediterraneus*. Bar scales represent 0·5 mm for *a* and *b*., 0·25 mm for *c*, *d* and *e*, and 0·1 mm for *f*.

Second maxilliped (Fig. 7*g*) : Exopod two-segmented, with 4 or 5 terminal setae. Endopod of 5 segments, the proximal unarmed. Epipod bilobed.
Third maxilliped (Fig. 7*h*) : Exopod two-segmented, with 4 terminal setae. Endopod of 5 segments, armed with numerous spines and setae and with the ischium expanded and carrying 4 or 5 teeth on the medial margin. Elongated epipod with 2 gill buds.

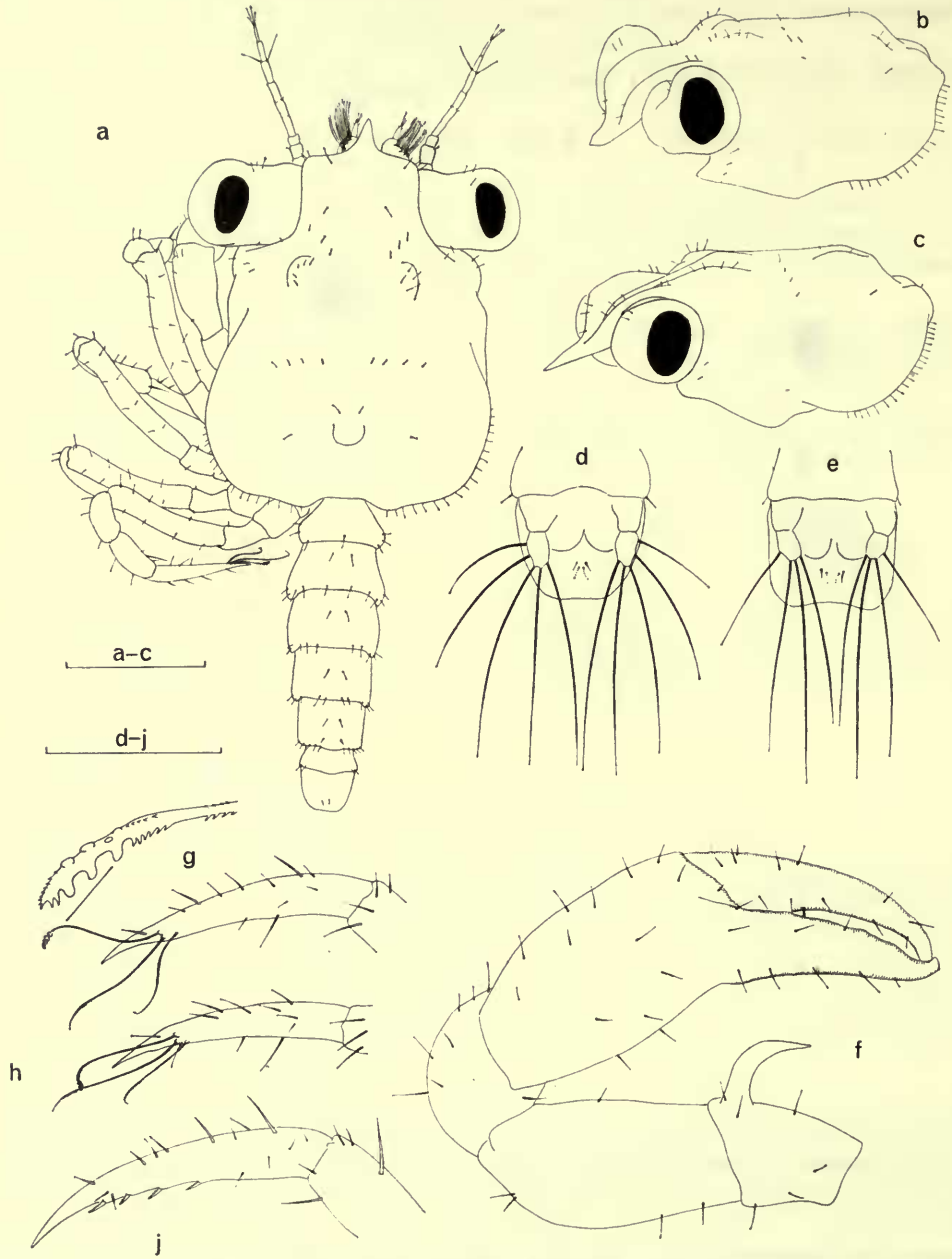

FIG. 6. *Carcinus* megalopa : (*a*) dorsal view, *C. maenas* ; (*b* and *c*) anterior-lateral views of carapace in *C. maenas* (*b*) and *C. mediterraneus* (*c*) ; (*d* and *e*) ventral views of telson and uropods in *C. maenas* (*d*) and *C. mediterraneus* (*e*) ; (*g* and *h*) dactyl of fifth pereiopod in *C. maenas* (*g*) and *C. mediterraneus* (*h*) ; (*j*) dactyl of second pereiopod, *C. maenas* ; (*f*) cheliped, *C. maenas*. Bar scales represent 0·55 mm for *a–c*, and 0·25 mm for *d–j*.

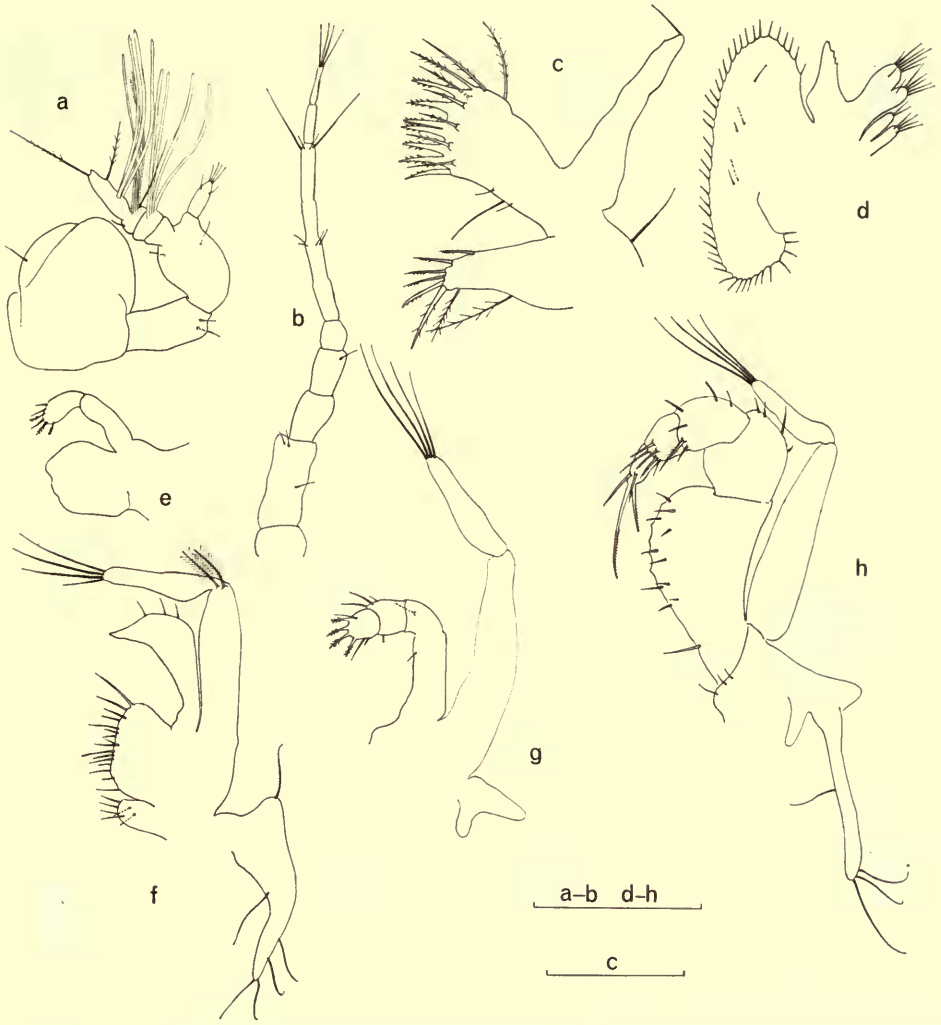

FIG. 7. *Carcinus maenas* megalopa; (*a*) antennule; (*b*) antenna; (*c*) maxillule; (*d*) maxilla; (*e*) mandible; (*f*) first maxilliped; (*g*) second maxilliped; (*h*) third maxilliped. Bar scales represent 0·1 mm for (*c*) and 0·25 mm for the remainder.

Pereiopods (Fig. 6*a* and *f–j*): Chelipeds with prominent ischio-basal hook. Legs 2–5 without coxal spines. Dactyl of leg 5 narrow (length/width ratio about 7 : 1), with 3 long, sub-terminal sensory setae.

Abdomen (Fig. 6*a*, *d* and *e*): Somites 2–4 with slightly variable pattern of dorsal setae, but usually with 5 pairs on the posterio-dorsal margin and 1 pair more anteriorly. Somite 5 with an extra pair. Telson with a pair of setae on both the dorsal and ventral surfaces, somewhat variable in shape, but with consistent differences between the two forms; in *C. maenas* the telson narrows posteriorly and

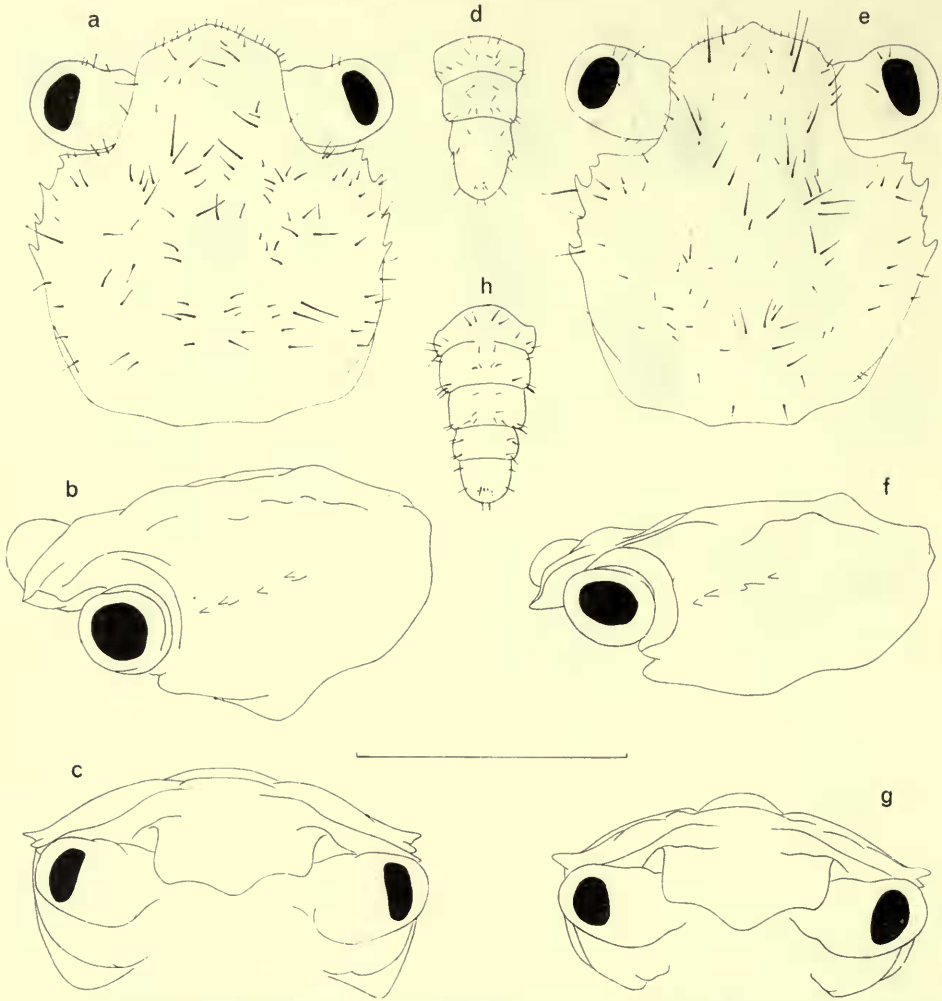

FIG. 8. *Carcinus* first crab stage : (*a–d*) *Carcinus maenas*, (*e–h*) *C. mediterraneus*, carapace (dorsal, lateral and frontal views) and abdomen. Bar scale represents 1·0 mm.

the posterior margin is usually straight or convex, and rarely concave ; in *C. mediterraneus* it is much more square, the lateral margins being more or less parallel or even diverging slightly, the posterio-lateral angles are more abrupt and the posterior margin is always concave, often markedly so.

Pleopods and uropods (Fig. 6*d*, *e*) : In both *C. maenas* and *C. mediterraneus* the pleopods are well developed with 3, rarely 4, coupling hooks on each endopod. But the setation of the exopods of these appendages and of the uropods was consistently different in the examples of the two forms examined and afforded the clearest means of separation. In general *C. mediterraneus* had fewer setae on the pleopods than did *C. maenas*, though since there was a good deal of overlap the setation of no single appendage would separate the two forms (see Table 2). When, however, the total

number of setae on the pleopods of the 5th abdominal somite and on the uropods was combined, a clear distinction was apparent, *C. maenas* megalopae always having a total of 32 setae on these appendages, while *C. mediterraneus* larvae never had more than 30.

TABLE 2

Setation of the pleopods and uropods in the megalopa larvae of *C. maenas* and *C. mediterraneus*, based on counts of five specimens in each case

	C. maenas		*C. mediterraneus*	
	Range	Mean	Range	Mean
Pleopod, somite 2	10–12	11·0	11–13	11·1
somite 3	11–12	11·9	11–12	11·8
somite 4	12–13	12·4	11–12	11·3
somite 5	11	11	9–11	9·8
Uropod	5	5	4–6	4·5

FIRST CRAB STAGE (Fig. 8)

Carcinus maenas: Carapace length 1·49–1·52 mm; carapace width (across tips of 5th anterio-lateral carapace spines) 1·36–1·47 mm.

Carcinus mediterraneus: Carapace length 1·49–1·57 mm; carapace width 1·38–1·50 mm.

Only two specimens of the first crab stage of *C. mediterraneus* were obtained so that little reliance can be placed on their comparison with the corresponding stage in *C. maenas*. However, in the material examined the two forms were extremely similar, the only differences being a slightly more prominent rostrum and dorsal carapace tubercles and a squarer telson in *C. mediterraneus* than in *C. maenas*. The other characters distinguishing the adults were not apparent in the first crab stage although *mediterraneus* has a slightly lighter build, the carapace being relatively a little narrower, than *maenas*.

DISCUSSION

Williamson's (1903) account of the development of *Carcinus maenas* includes a great deal of detail and, in this respect, has rarely been equalled by any subsequent description of decapod larvae. His larvae were generally a little larger than those reared from the Plymouth and Brighton females reported here, but otherwise the two accounts agree almost without exception. This agreement confirms, if such confirmation was needed, firstly the accuracy of Williamson's observations and secondly that his specimens of the third and fourth zoeal stage and of the megalopa, all of which he obtained from the plankton, were correctly identified. Lebour's (1928) account is much less complete, but where comparisons are possible her descriptions also agree with the reared British larvae. Both of these authors mention the loss in the late zoeae of two of the three telson fork spines which are present in the early stages, whereas a second spine was almost always present in our stage four larvae. However, this second spine is extremely small and difficult to see, so that it was probably simply missed by Williamson and Lebour.

The earlier accounts also agree with the present description of the British *Carcinus* larvae in those features which distinguish them from the Mediterranean material,

and particularly in the setation of the abdominal appendages of the megalopa. Williamson, for instance, gives the setation of the exopods of the pleopods as 11, 11–13, 12 or 13, and 11 respectively, while both he and Lebour report 5 setae on the uropods as opposed to the 4 setae usually found on our Mediterranean larvae. The account of these Mediterranean larvae is based on material obtained from only one brood so that the distinctions noted might simply reflect individual variation. But the agreement between all the available descriptions of British larvae argues against this and suggests that definite genetic differences exist between the Atlantic and Mediterranean *Carcinus* populations.

Whether these differences are sufficient to warrant the two populations being accorded full specific status is, however, debatable, for they appear to be allopatric, *C. mediterraneus* never having been reported from outside the Mediterranean, while *C. maenas* is not known from within it. In these circumstances the ultimate criterion of the absence of interbreeding between overlapping populations cannot be applied and any opinion about their taxonomic status must be somewhat subjective.

Comparing the degree of difference between the two allopatric forms with that between undoubtedly distinct species in the same group does not provide very conclusive evidence. For although portunid crabs are often quite difficult to separate as juveniles, there are usually more distinct differences between the mature forms than those noted between *Carcinus maenas* and *C. mediterraneus*, and in the larval stages the situation is similar. In terms of the number of species of which larvae have been described, the best known portunid genus is *Macropipus*, and although the known larval stages of this genus are all very similar, detailed examination has generally revealed better distinctions between the species than those between the two types of *Carcinus* larvae described here (Rice & Ingle, 1975).

It seems, then, that there is no very good larval evidence to support the separation of *maenas* and *mediterraneus* as distinct species, despite the existence of consistent differences between the adults. A study of both adults and larvae from the vicinity of the Straits of Gibraltar, both in the Mediterranean and in the Atlantic, would be of considerable interest, though if no area was found in which the two forms co-exist, or intergrade, the problem would still be unresolved. Since the adults are so readily distinguishable, however, it seems worth while at present to maintain their specific status, but if they are ultimately shown to be totally allopatric the most sensible course would probably be to consider them to be subspecies, as was apparently the intention of Czerniavsky (1884) when he divided *C. maenas* into the two varieties *mediterranea* and *septentrionalis* (see Holthuis & Gottlieb, 1958). For as Mayr, Linsley & Usinger (1953) point out, the use of trinominals has the advantage in such situations of conveying the important information that the two forms are closely related and geographically separated.

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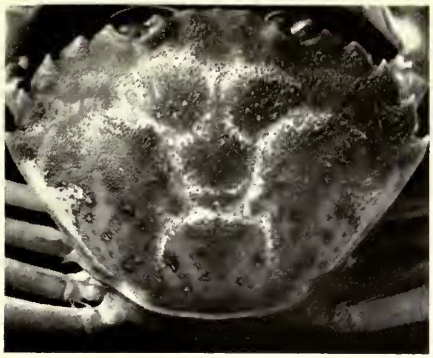
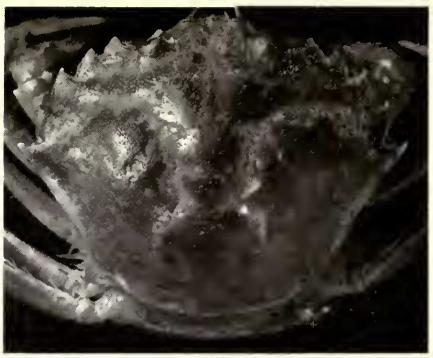
PLATE 1

Dorsal and posterior views of the carapace and of the outer face of the right cheliped of the female *C. maenas* from Brighton (A, B and C) and of the female *C. mediterraneus* from Salammbo (D, E and F).



A



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